1.11 BIOTIC CONTROLS OVER THE FUNCTIONING OF DESERT RIPARIAN ECOSYSTEMS

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1. ABSTRACT

Functional traits of dominant riparian tree species were evaluated at several sites along the San Pedro River and Rincon Creek drainages in southeastern Arizona, USA and northern Sonora, Mexico. The sites differed in stream flow characteristics, groundwater depth, and vegetation structure. Our intent was to examine temporal and habitat related variation of biologically mediated processes that determine ecosystem and basin scale carbon and water fluxes. Tree sap flow, water potential, water sources, stomatal conductance, and photosynthesis were determined for several dominant woody perennial plants at key periods over the 1996 and 1997 growing seasons. Measurement periods encompassed variations in atmospheric VPD, surface moisture availability, and groundwater depth. Initial results suggest that processes governing tree and stand level transpiration, water extraction from soil and groundwater, and photosynthetic carbon gain within desert riparian ecosystems vary by stream type, species, and season.

2. INTRODUCTION

Riparian ecosystems of arid and semi-arid regions contain a disproportionate share of regional biodiversity and play a dominant role in regional water and energy balance (Maddock *et al*., this issue), but are extremely sensitive to perturbations that affect groundwater and surface water supply to dominant plants of streamside vegetation (Stromberg 1993, Busch *et al*. 1992). Current activities of the Semi-Arid Land Surface Atmosphere (SALSA) Program (Goodrich *et al*., this issue) include investigations on processes controlling seasonal and interannual fluxes of water from these strips of forested vegetation on the San Pedro River and adjacent areas (Hipps *et al*., this issue), and development and calibration of protocols for monitoring these processes using remotely sensed observations (Moran *et al*., this issue). Increased understanding of the functioning of these systems will support ongoing efforts to sustain the biological and hydrological resources of this region and similar arid and semi-arid basins worldwide.

Principle factors controlling the functioning of riparian ecosystems include regional climate, system hydrology, disturbance, and dominant plant functional types (Fig. 1). These controlling factors are interactive; positive and negative feedbacks exist between the ecosystem traits and controlling factors. Controlling factors operate within potentials set by time, global climate, topography, parent material, and potential biota (Jenny 1941, Chapin *et al*. 1996).

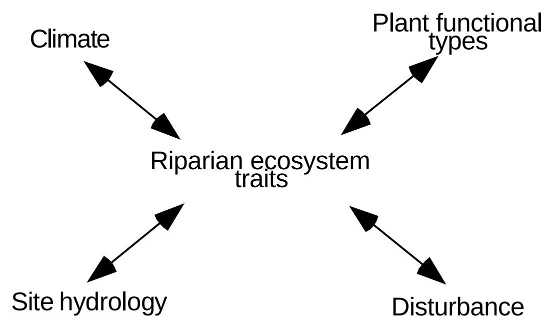

Figure 1. Conceptual diagram showing interactive factors controlling riparian ecosystem traits (adapted from Chapin *et al*. 1996).

Ecosystem traits such as carbon and nutrient flow or evapotranspiration affect and are affected by the composition and function of dominant plant species. This interactive control that dominant plants have over ecosystems can operate at different time frames and across spatial scales ranging from leaves or whole plants to landscapes and regions. Interactive control from the biotic component of ecosystems has been the focus of recent attempts at understanding how to sustain important processes and encourage ecosystem stability in the face of natural and human related environmental perturbations (Chapin *et al*. 1996).

The plant functional type (PFT) concept has emerged as a useful way to organizing plant species with similar impacts on ecosystem processes into manageable and meaningful categories. Useful traits for a PFT classification in riparian zones emphasizing hydrologic and biotic resources should include plant water sources (groundwater, soil water), rates and processes of canopy transpiration and energy exchange, stomatal responses to climatic fluctuations, plant hydraulic architecture, and drought tolerance. For example, responses of stomata to climatic fluctuations and feedback with the boundary layer (*sensu* Jarvis and McNaughton 1986) may differ among patches of riparian vegetation dominated by different functional types, thereby influencing rates or patterns of transpiration (Meinzer *et al*. 1995)

Site hydrology and geomorphology could also shape the nature of plant controls on riparian

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ecosystem processes by affecting establishment and density of key plant species or by altering tree hydraulic architecture, canopy structure, or stomatal response by acclimation or plasticity . Thus, a PFT description of dominant plant species in riparian zones should recognize species-environment responses and account for stream type (ephemeral, perennial, etc.) or habitat condition. This is similar to the concept of “norms of reaction” that are useful for predicting ecological and evolutionary responses of genotypes, populations and species (Stearns 1989) to environmental heterogeneity, but are applied here to changes in species’ functional roles at the ecosystem level.

Over long time frames, disturbance (flooding, grazing, land clearing) can promote or degrade processes controlling stability of riparian ecosystem traits. Occasional flooding provides the microhabitat conditions needed for continued establishment of key riparian tree species or PFTs (Stromberg 1993). On the other hand, intensive grazing may enhance runoff and site aridity, thereby shifting the competitive advantage from one PFT to another and also reducing transpiration. These land surface changes can potentially alter regional patterns of precipitation and temperature (Charney *et al*. 1977). Shifts from grass to shrub cover in arid basins due, in part, to grazing disturbance, has occurred in many southwestern watersheds during this century (Archer *et al*. 1988) and has implications for regional and global scale land surface-atmosphere interactions (Melillo *et al*. 1996). It is still unclear how interactions between the grass and shrub functional types in arid and semi-arid basins determine patterns of energy exchange and groundwater, surface water, and transpiration fluxes.

Regional climate controls vegetation structure, phenology, and physiology and, therefore, shapes functioning of ecosystems. Vegetation, in turn, governs water and temperature gradients, surface roughness, and albedo and influences local and regional climate through energy and water exchange with the atmosphere. The role of stomatal control on stand and regional scale evapotranspiration rates is debated as is the exact response mechanism of stomata to environmental fluctuations (Cowan 1977, Jarvis and McNaughton 1986, Monteith 1995). Consequently, the nature of interactions between vegetation and regional climate are uncertain, especially over arid and semi-arid heterogeneous surfaces (Toth *et al*. and Hipps *et al*., this volume).

This paper provides an overview of SALSA Project investigations aimed at understanding patterns and magnitudes of biotic controls over riparian ecosystem traits emphasizing those processes operating at the scale of small patches of vegetation, whole plants, and individual plant organs. We addressed whether plant functional types were discernible among the dominant woody component of riparian ecosystems with respect to their impact on groundwater, soil water, and evapotranspiration interactions. We asked the following specific questions: 1) Does the magnitude of stomatal control on canopy transpiration vary among dominant tree species or among sites with different hydrologic characteristics? 2) Does variation in groundwater availability influence the proportion or magnitude of surface water use by these trees? 3) How does variation in grass cover beneath shrubs relate to patterns of soil water extraction and transpiration? 4) Is tree hydraulic architecture an important determinant of ecosystem-level water fluxes and does this vary among species or sites?

3. **APPROACH AND METHODS**

3.1 *Shrub/grass interactions*

To address potential impacts of changes in cover of shrub and grass functional types, the team from OSTROM/IMADES based in Hermosillo, Mexico has launched a series of modeling and measurement activities along a sharp vegetation gradient in an upland section of the San Pedro River in Mexico near Cananea. The general nature of the gradient which ranges from mesquite dominated microsites to mesquite/grass microsites differs from other riparian sites investigated by SALSA in that the dominant plant component did not include a cottonwood/willow canopy. Measurement activities focusing on mesquite water sources and stem sap flow lead by J.-P. Brunel were designed to characterize the proportion and quantity of water transpired by mesquite where grass cover was either abundant or lacking (Table 1). These measurements will provide insight into how transformations in shrub/grass cover that has occurred over very large scales in the southwest may have altered key processes in the hydrology of arid basins. Particularly, these measurements will provide details on feedbacks (Fig. 1) that contribute to basin climate, hydrology, and riparian ecosystem traits.

3.2 *Riparian tree functional types*

Another set of measurement activities focused on plant functional traits within more mesic river vegetation on the US side of the border, predominantly along the San Pedro River (Table 1). The objectives here were to characterize variation in plant function across a range of riparian hydrological conditions and among dominant woody species.

3.2.1 *Sites*

We characterized tree functional traits at three mesic riparian sites along the San Pedro River and at one site on Rincon Creek east of Tucson, AZ. The sites differed in stream flow characteristics, groundwater depth, and vegetation structure and represented two intermittent stream reaches (Rincon Creek and San Pedro River), one ephemeral tributary of the San Pedro River (Escapule Wash), and one perennial reach of the

Table 1. Summary of measurement activities on or near the San Pedro River in southeastern Arizona, and northern Sonora, Mexico to investigate plant functional traits and ecosystem processes in desert riparian ecosystems.

Site	Stream type	Vegetation structure[2]	Plant water relations[3]	Leaf gas exchange[4]	Sap flow[5]	Species[6]
Cananea, SPR[1], Mexico	upland, intermittent	LAI	Ψ_s, δ_{H2O}		HB	A
Lewis Springs, SPR, USA	perennial	LAI, DBH	Ψ_s, Ψ_p, δ_{H2O}	g_s, A, $\delta^{13}C$	HB, HP	ABCD
Boquillas, SPR, USA	intermittent	DBH	Ψ_s, Ψ_p, δ_{H2O}	$\delta^{13}C$		ABC
Escapule Wash, USA	ephemeral	LAI, DBH	Ψ_s, Ψ_p, δ_{H2O}	g_s, A, $\delta^{13}C$	HB, HP	ABCD
Rincon Creek, USA	intermittent		Ψ_s, Ψ_p, δ_{H2O}	$\delta^{13}C$		ABCDEF

[1] SPR = San Pedro River
[2] LAI = leaf area index, DBH = bole diameter at 1 m
[3] Ψ_s = soil matric potential, Ψ_p = plant water potential, δ_{H2O} = plant and source hydrogen and oxygen stable isotope ratio
[4] g_s = stomatal conductance, A = photosynthetic rate, $\delta^{13}C$ = leaf carbon-13 isotope ratio
[5] HB = heat balance method, HP = heat pulse method
[6] A = mesquite, B = cottonwood, C = willow, D = seep willow, E = ash, F = hackberry

San Pedro. The Rincon Creek site had greater tree species diversity than did sites on the San Pedro River.

3.2.2 *Vegetation structure*

Extensive vegetation surveys were conducted at three sites; Lewis Springs (LS), Boquillas (BQ), and Escapule Wash (EW) to determine size class distribution and basal area dominance of riparian tree species focusing on mesquite (*Prosopis velutina*), Frémont cottonwood (*Populus fremontii*), and Goodding willow (*Salix goodingii*) (see Schaeffer and Williams, this volume for details). Leaf area index (LAI) was determined at two of these sites (ephemeral EW and perennial LS) at monthly intervals through the 1997 growing season using a LICOR LAI2000 canopy analyzer.

3..2.3 *Plant water relations*

Tree sap, groundwater, soil water, stream water, and precipitation were sampled for stable isotopic composition ($\delta^{18}O$, $\delta^{2}H$) to determine water sources (see Snyder and Williams, this volume for details). At Rincon Creek, six woody species were sampled in August, 1996. At the San Pedro sites we sampled at several periods over the growing season (April, June, July, August, September) in 1997, but made measurements only on mesquite, cottonwood, and willow. Measurements on seep willow were added in June and August at LS and EW. Predawn and midday plant water potential and soil moisture measurements were made concurrently with isotopic sampling. Tree water potential measurements along with leaf and whole plant transpiration measurements (below) were used to assess variation in tree hydraulic conductivity among sites and species.

3.2.4 *Leaf gas exchange*

We assessed diurnal courses in stomatal conductance, photosynthesis, and leaf internal CO_2 concentrations using a portable gas exchange system (PP Systems, CIRAS-1). These instantaneous measurements were made at EW and LS during three key periods over the growing season in 1997 (April green-up, June drought, and August monsoon) to capture potential changes in stomatal control on transpiration and stomatal sensitivity to environmental fluctuations. Spot measurements of leaf temperature were made with a hand-held infrared thermometer. We used a large 25 m boom lift to access the upper canopy of cottonwood and willow for gas exchange and leaf temperature measurements. Spot and continuous measurements of photosynthetically active radiation, humidity, and air temperature were made with the leaf chamber sensor head and a micrometeorological tower erected at the sites.

Flux-integrated gas exchange properties were investigated using $\delta^{13}C$ values of leaf tissues. Leaves were collected from trees at all four riparian sites used in this aspect of the SALSA Project. $\delta^{13}C$ values of leaf organic matter record the internal to ambient CO_2 concentration ratio (c_i/c_a) over the time period of leaf growth (Farquhar *et al*. 1989). c_i/c_a is related to stomatal limitation of photosynthesis and water-use efficiency, thus $\delta^{13}C$ values provide a convenient estimation of relative stress and drought tolerance in desert plants (Williams and Ehleringer 1996, Ehleringer 1993).

3.2.5 *Sap flow*

Diurnal courses of sap flow through terminal branches and whole trees of cottonwood and willow were assessed at two sites (EW and LS) during intensive field campaigns in April, June, August, and October, 1997. In addition to estimating stand transpiration (Schaeffer and Williams, Moran *et al.*, Qi *et al.*, this issue), sap flow measurements were conducted to evaluate species and site differences in plant hydraulic architecture. Heat pulse sensors were installed to estimate tree transpiration (see Schaeffer and Williams, this volume for details). Additionally, stem heat balance gauges (Dynamax, SGA-10, SGA-13, SGA-16) were installed on small branches of two trees of each of cottonwood and willow in June and August. Transpiration recorded from the heat balance gauges were expressed per unit leaf area supported by the branch and together with measurements of stomatal conductance and bulk air VPD (see above) we estimated the stomatal coupling coefficient (Ω, Jarvis and McNaughton 1986) under a variety of conditions.

4. INITIAL RESULTS AND DISCUSSION

Isotopic variation among six woody tree and shrub species at an intermittent stream site (Rincon Creek) revealed discreet functional groupings based on water sources used by the plants ($\delta^{18}O$) and leaf gas exchange properties (Fig. 2). Cottonwood, willow, and the shrub seep willow appear to utilize mostly groundwater, whereas a significant proportion of water utilized by hackberry, ash and mesquite was from soil. $\delta^{13}C$ values of leaves and xylem water $\delta^{18}O$ were correlated (r^2=0.93), indicating that stomatal conductance, transpiration rates, tolerance to drought, and water-use efficiency may differ between functional types that use different water sources in these riparian areas.

Cottonwood at the perennial Lewis Springs site in 1997 used only groundwater and did not take up surface water even following a large rain and flood event in August (see Snyder and Williams, this volume for details). Interestingly, a larger proportion of water used by mesquite at this site was from groundwater compared to that for mesquite at intermittent and ephemeral stream sites (Snyder and Williams, this volume).

Large cottonwood trees in this semi-arid region transpire water at very high rates. The large (70 cm DBH) cottonwood tree depicted in Figure 3 lost up to 60 kg of water h^{-1} in August, 1997 during the SALSA field campaign at Lewis Springs (see Schaeffer and Williams for more details). Diurnal variations in transpiration from this tree were strongly influenced by fluctuations in photosynthetic photon flux density at the site (Fig. 3). Maximum daily transpiration rates for several representative cottonwood trees at Lewis Springs were approximately 12% lower during the June observation period compared to that in August, reflecting differences in maximum daily VPD (data not shown). Water potential gradients between the rhizosphere and leaf during maximum transpiration, however, were higher in June (1.2 MPa) than in August (1.0 MPa) suggesting that root-to-leaf pathway hydraulic conductivity may have increased from early to late summer. Changes in whole plant hydraulic conductivity may have resulted from decreases in tree leaf area or from construction of new roots or xylem as the season progressed. Tree hydraulic architecture, in general, may set limits on maximum transpiration fluxes especially if stomatal conductance or leaf surface area are regulated to prevent damage from cavitation inducing xylem water tensions (Tyree and Sperry 1988).

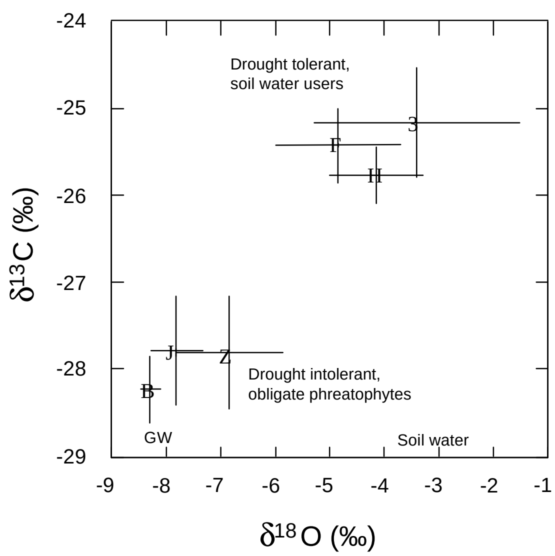

Figure 2. Relationship between the $\delta^{18}O$ of plant xylem water and $\delta^{13}C$ of leaf tissue for dominant woody plants at an intermittent stream (Rincon Creek) in southern Arizona in August, 1996. Plant species are seep willow (B *Baccharis glutinosa*), Frémont cottonwood (J *Populus fremontii*), Goodding willow (Z *Salix goodingii*), velvet ash (H *Fraxinus velutina*), velvet mesquite (F *Prosopis velutina*), and netleaf hackberry (3 *Celtis laevigata*). Data are means and standard error bars (n=3-5).

Further analysis of these data will address whether tree hydraulic conductivity differs among species and sites, if functional groupings based on water source and leaf carbon isotope ratios hold for the dominant species across sites, and if stomatal control of canopy transpiration differs among species or sites.

5. SUMMARY

Dominant plants, interacting with disturbance, regional climate, and site hydrology control temporal and spatial dynamics of riparian ecosystem properties such as evapotranspiration, carbon gain, and energy flow. The objective of our SALSA Project investigation was to characterize variation in key physiological processes (among sites and species) that determine ecosystem and basin hydrologic fluxes. Initial results suggest that patterns of water extraction, transpiration, and photosynthetic gas exchange vary among dominant plant species and these physiological processes are modified by site conditions. We recommend a plant functional type classification of dominant riparian species that reflects dynamic functional roles for species across sites or through time as site conditions change. This is analogous to the "norm of reaction" concept and recognizes that plasticity and acclimation can alter key functional traits that have implications for ecosystem or regional energy and material fluxes.

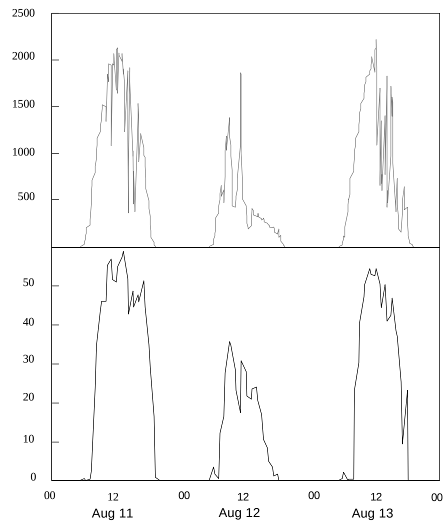

Figure 3. Diurnal course of photosynthetic photon flux density (PPFD) and transpiration from a large cottonwood tree at Lewis Springs during the August, 1997 SALSA integrated measurement period.

6. ACKNOWLEDGMENT

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